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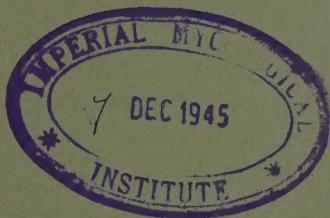
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Interpreting Botanical Progress

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# THE BOTANICAL REVIEW

VOL. X

APRIL, 1944

No. 4

## PRESENT-DAY CLASSIFICATION OF ALGAE<sup>1</sup>

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### INTRODUCTION

During the latter part of the nineteenth century it was customary to recognise four main classes of algae (32, 52, 54, 152, 154): Chlorophyceae, Phaeophyceae (Melanophyceae), Rhodophyceae, Cyanophyceae (Schizophyceae, Myxophyceae). Diatoms and Peridinieae, likewise accepted as algae, were sometimes treated as separate groups (32, 139, 157) and sometimes classed among the Phaeophyceae (152, 154). Various authors (152, 154) also included in the latter a number of the Flagellata, now largely comprised in the Chrysomonadineae, while in the first edition of the "Natürliche Pflanzenfamilien" (128) the Flagellata as a whole were given a brief though very useful consideration within the compass of the Thallophyta. Most writers, however, altogether ignored the bulk of the Flagellata. This was an altogether illogical attitude, so far as the holophytic members of this series were concerned, for even at this period *Chlamydomonas* and other green starch-producing Flagellata (*Pandorina*, *Eudorina*) were included among the Chlorophyceae.

The modern era in algal classification commences with the removal by Luther (86) in 1899 of certain genera, hitherto referred to Chlorophyceae, to a separate class, the Heterokontae, distinguished *inter alia* by yellow-green chloroplasts, formation of oil as a photosynthetic product, and two unequal anterior flagella on the motile stages. The ground had been prepared by Borzi (16, 199) and Bohlin (12) who had grouped some of the genera (*e.g.*, *Botrydiopsis*, *Ophiocytium*, *Conferva* = *Tribonema*,) as Confer-  
vales, but it was the discovery of a flagellate, *Chloramoeba* (13),

<sup>1</sup> In general only the broader aspects of classification of algae are taken into consideration, since a detailed discussion of the many problems relating to the placing of individual genera would unduly increase the length of this article.



and of a palmelloid type, *Chlorosaccus* (86) showing heterokontan characteristics, that betrayed the existence of a larger entity than could be accommodated in a mere subdivision of the Chlorophyceae. Recognition of the taxonomic differences between the latter and the Heterokontae, as well as of the fact that each of these classes was distinguished by a definite type of flagellate organism, led to the adoption of a new attitude towards the heterogeneous group of motile forms known to zoologists as Flagellata. The new outlook found a fuller expression in a later paper by Bohlin (14) and, for English readers, in F. F. Blackman's (6) article on "The primitive algae and the Flagellata", while Blackman and Tansley's "Classification of the Green Algae" (7) was an exposition of the new point of view so far as the green and yellow-green algae were concerned. In a reprint published the following year (8) the designation "Isokontae" was adopted for the Chlorophyceae and remained in vogue for a considerable time, although more recent writers have reverted to the old name, and "Isokontae" has fallen into disuse. The desire for a uniform terminology for the various algal classes has also led in some quarters (41, 136) to acceptance of the name "Xanthophyceae" (3) for the Heterokontae, and this is followed in the present article.

#### INTERRELATIONS OF FLAGELLATA AND ALGAE

A further step leading to the present-day basis of classification of algae was afforded by an important memoir of Klebs (64) in which he described a number of coccoid types showing at certain stages of their development all the essential characteristics of the Peridinieae. It thus became apparent that, also in this group of dominant flagellate types, forms with an algal organisation had been evolved. It was left to Pascher, however, to carry to its logical conclusion the attack on the Flagellata initiated by the work of Bohlin, Luther and Klebs. In a striking paper published in 1914 (95) he showed not only that a close relation between flagellate and algal types was patent among Chlorophyceae, Xanthophyceae and Peridinieae, but that similar relations existed between the flagellate forms grouped by Senn (128) as Chrysomonadineae and Cryptomonadineae and corresponding algal forms briefly considered in Pascher's paper. The three classes with predominant flagellate organisation thus distinguished were designated Chrysophyceae (in-

cluding the Chrysomonadineae), Dinophyceae (including the Peridinieae) and Cryptophyceae (including the Cryptomonadineae).

The flagellate members of each of these classes as well as of the Chlorophyceae and Xanthophyceae, possess distinctive accessory chromatophore pigments and produce different photosynthetic products, implying for each class a distinctive metabolism; they are also distinguished by their morphological features and especially by the nature and orientation of the flagella. Each class also includes a variety of palmelloid, coccoid and filamentous types, such as have long been known among the Chlorophyceae; among Xanthophyceae, Chrysophyceae and Dinophyceae their number has been appreciably increased by later communications of Pascher (98, 99, 102, 105, 107). Such algal forms show the physiological characteristics (pigmentation, photosynthetic products) distinctive of the flagellate types of their class, and many of them propagate by motile reproductive units which, also in their morphological characters, closely resemble the flagellate members. Pascher was the first to bring out clearly the essential parallelism between the different classes, a parallelism which is reflected in the broad classification given below and which, with some modifications, has been generally adopted. The flagellate, palmelloid, coccoid, filamentous and siphonous types were relegated to separate orders, as indicated in the following synopsis, taken from the 1914 paper and slightly modified in the light of subsequent knowledge:

	Chlorophyceae	Xanthophyceae (Heterokontae)	Chrysophyceae	Dinophyceae	Cryptophyceae <sup>2</sup>
Flagellate	Volvocales	Heterochloridales	Chrysomonadales	Dinoflagellata	Cryptomonadales
Palmelloid	Tetrasporales	Heterocapsales	Chrysocapsales	Dinocapsales	Phaeocapsales
Coccoid	Protococcales (Chlorococcales)	Heterococcales	Chrysosphaerales	Dinococcales	Cryptococcales
Filamentous	Ulotrichales	Heterotrichales	Chrysotrichales	Dinotrichales	.....
Siphonous	Siphonales	Heterosiphonales	.....	.....	.....

Of the pigmented holophytic Flagellata distinguished by Senn (128) there remain only two series—the Chloromonadineae and

<sup>2</sup> The Cryptotrichales distinguished in the 1914 paper subsequently proved to be members of Chrysophyceae.

Euglenineae—in which, so far as present knowledge goes, no algal types have been evolved. The few rather complex motile unicells (e.g., *Vacuolaria*, *Gonyostomum*) included in the Chloromonadineae appear to have no affinities with the other groups, and future investigations must establish their exact status. The holophytic Euglenineae (*Euglena*, *Trachelomonas*, *Phacus*, etc.) exhibit no characteristics that support their inclusion among the Protozoa, and the zoological terminology suggestive of a process of holozoic nutrition is quite unwarranted and deplorable. As in other flagellate groups (Volvocales, Chrysomonadales, 112), there has been considerable evolution of colourless types, but the majority of them (Astasiaceae) are pure saprophytes and the peculiar holozoic nutrition of Peranemaceae is clearly derivative. There can be no doubt that the Euglenineae are a group parallel to the flagellate series of the five algal classes referred to above, and future research may yet disclose true algal representatives of this class. Until these are discovered, use of the names “Euglenophyceae” (135) or “Euglenophyta” (104) is debatable.

#### CLASSIFICATION OF FLAGELLATE AND COCCOID FORMS

Certain differences of opinion as regards classification of the flagellate, palmelloid and coccoid types may well be discussed at this stage. Various authorities (41, 92) do not refer the palmelloid members to distinct orders, regarding them merely as modifications of the flagellate type resulting from the well known tendency of forms like *Chlamydomonas* to assume under certain circumstances a temporary *Palmella*-stage. In both *Chlamydomonas* (Chlorophyceae) and *Chromulina* (Chrysophyceae), species are known in which this palmelloid phase is dominant, although in such instances the individual cells usually retain their flagella so that the motile condition is readily readopted. Fritsch (41, 162), therefore, classes the palmelloid types as Tetrasporineae, Heterocapsineae, Chrysocapsineae, etc., which constitute suborders of the Volvocales, Heterochloridales, Chrysomonadales, etc., the flagellate members being grouped in the suborders Chlamydomonadineae, Heterochlorineae, Chrysomonadineae, etc.

A not uncommon modification of the motile flagellate cell, especially in those classes in which it is devoid of an enveloping membrane, is constituted by the permanent adoption of an amoeboid or



rhizopodial habit. In his 1914 paper Pascher (95) placed such forms as suborders of Chrysomonadales and Heterochloridales, but in a later communication (104), dealing with the broad classification of algae, they rank as separate orders (*cf.* also 135). Fritsch (41), however, treats them in the same way as the palmelloid types, classing them as Heterorhizidineae, Rhizochrysidineae, Rhizodinineae among Heterochloridales, Chrysomonadales and Dinoflagellata, respectively. Such differences in taxonomic outlook are a matter of individual opinion, but in the view of the writer, inclusion of the palmelloid and rhizopodial forms in the same order as flagellate types affords a better expression of their true affinities and thus a more natural classification.

A number of genera (*e.g.*, *Chlorangium*, *Prasinocladus* = *Chlorodendron* Senn) producing colonies with a branched dendroid habit, in which the individual cells readily become detached and assume a temporary motile habit, have long been known among Chlorophyceae. In conformity with the practice adopted by Wille (165), Blackman and Tansley (7) placed them among the palmelloid forms, and this has been followed even in recent times (113, 135). There is, however, no evidence of any direct connection with the palmelloid type, as was first claimed by Oltmanns (90, 136) who referred these forms to a distinct family, the Chlorodendraceae (Chlorangiaceae of Smith (135)), while Fritsch (41, 162) establishes for them a separate suborder, the Chlorodendrineae, and refers equivalent types among Xanthophyceae (*Mischococcus*) to the Heterodendrineae. Pascher (104, 327) groups the dendroid green algae in a separate subdivision (Chlorangiales) of his Tetrasporineae. It should be added that among the forms at present classed with *Chlorangium* and *Prasinocladus* among Chlorodendrineae there are several aberrant types (*Ecballocystis*, *Hormotila*) that may prove to belong to an altogether different affinity, the Hormotilaceae of Pascher (104, 327).

In those classes in which a wide variety of flagellate genera has become known, the need for a taxonomic grouping has resulted in a diversity of schemes, several of which are open to criticism. Among Volvocales the marked contrast in cell-structure exhibited by certain species of *Sphaerella* (*Haematococcus*) as compared with *Chlamydomonas* (24) has led diverse recent authorities (41, 135, 161) to recognise two separate families, Chlamydomonadaceae

and Sphaerellaceae. Better knowledge of *Sphaerella* indicates that it is probably derivative from *Chlamydomonas*, but the two generic types remain sufficiently distinct to warrant reference to separate families. Whether *Chlorogonium* is justifiably referred to Sphaerellaceae remains to be seen (cf. 135, 346).

*Stephanosphaera* is usually placed in the same family as *Sphaerella*, while there is difference of opinion whether *Volvox* should be referred to it. Many types of *Volvox* certainly differ very profoundly in cell structure from that of the majority of other colonial Volvocales, and the approximation to *Sphaerella* by no means lies only in the presence of rhizopodial processes emanating from the main body of the protoplast. The main series of colonial Volvocales (*Gonium*, *Pandorina*, *Eudorina*, *Pleodorina*, etc.) is referred by many to a family (Volvocaceae) distinct from that harbouring the unicellular forms, but the writer (41) dissents from this view. It may be pointed out that it is hardly logical to include *Stephanosphaera* in Sphaerellaceae and to exclude *Gonium* and other genera from Chlamydomonadaceae. Moreover, there can be no question that most species of *Volvox* differ far more profoundly from the other Volvocaceae than the latter do from *Chlamydomonas*.

The flagellate members of Chrysophyceae exhibit a greater degree of variety in the motile apparatus than do the corresponding types among Chlorophyceae and Xanthophyceae. Senn (128) first introduced the classification of Chrysomonadineae into Chromulineae with one, Hymenomonadeae (Isochrysideae (94)) with two equal, and Ochromonadeae with two unequal flagella, to which in recent times have been added the Prymnesieae (23) with one short and two long flagella. Such a grouping, although taxonomically useful in the present state of our knowledge, is hardly likely to be a natural one. The less specialised members of Isochrysideae and Ochromonadeae are likely to be closely related. The two equal flagella of the former are probably always dissimilar in structure (109, 156), in the same way as are the unequal flagella of the Ochromonadeae and Xanthophyceae (155). It is possible, moreover, that the uniflagellate condition of the Chromulineae may have resulted from loss of a flagellum. Certain species of *Chromulina* certainly approximate closely to certain types of *Ochromonas*. The deficiencies of the existing basis of classification have become particularly patent in relation to the coccoid Chrysophyceae, where



vegetatively similar forms commonly propagate by zoospores with contrasting types of flagellation. It seems probable that in the future the flagellate Chrysophyceae will have to be grouped more particularly with reference to their cell structure, especially that of the envelope.

Pascher (95) separated from the main class of the Dinophyceae a series, the Desmokontae, which appear on the whole to show a more primitive organisation and are possibly related to the Cryptomonadineae. They include a number (*Desmomastix*, *Pleromonas*, *Haplodinium*) of relatively simple flagellate types (Desmomonada-ceae) with a pair of apically inserted, dissimilar flagella, a palmeloid type (*Desmocapsa*, (122, 11)), as well as the more specialised marine family Prorocentraceae and the Dinophysiales, which last approximate more closely to the Dinoflagellata. Fritsch (41) classes these Desmokontae as a subdivision of the Dinophyceae, the typical members of which are grouped in the Dinokontae. Space does not permit further discussion of the detailed classification of the latter.

Most authorities have assumed a fairly close relationship between the flagellate and coccoid types in the classes of algae at present under consideration. Some (*e.g.*, 8, 113, 161) have in fact included the Volvocales and Chlorococcales in a common group<sup>3</sup>, and it can not be denied that a case could be made out for such a practice among both Chlorophyceae and other algal classes. Those coccoid forms that reproduce by zoospores are in part at least closely related to motile flagellate types, and instances of the retention of essential features of the motile individual (stigma, contractile vacuoles) by the coccoid cell are indeed known in practically all classes under discussion. The discovery of such forms among Chlorococcales led Korschikoff (66, 490; 69) to establish the group Vacuolatae, although this means putting too much stress on a single character; moreover, recent work on *Chlorococcum* (47, 375) tends to show that the presence of contractile vacuoles may depend on the environment. Despite the obvious affinities, the contrast between the free-moving flagellate and coccoid habits is significant of the evolutionary trend that probably initiated the

<sup>3</sup> This is called Protococcales. Since it is now almost generally agreed that *Protococcus* (*Pleurococcus*) is a reduced filamentous member allied to the Ulotrichales or Chaetophorales, it is time that the designation Protococcales be altogether abandoned for the coccoid green types and the name Chlorococcales, introduced by Fritsch (162; *cf.* also 135), substituted.

SYNOPSIS OF SOME OF THE MORE RECENT SYST  
(The sequence of orders and families is not

West, 1916	Printz, 1927	Oltmanns, 1922
Protococcales (Isokontae)	Euchlorophyceae	Chlorophyceae
Volvocineae	Protococcales	Volvocales
Polyblepharidaceae	Volvocaceae	Polyblepharidaceae
Sphaerellaceae		Chlamydomonadaceae
Volvocaceae		Phacotaceae
		Volvocaceae
Tetrasporineae		
Palmellaceae	Tetrasporaceae	Tetrasporaceae
		Chlorodendraceae
Protococcaceae	Chlorococcaceae	Protococcales
Dictyosphaeriaceae	(Protococcaceae)	Protococcaceae
Autosporaceae	Pleurococcaceae	
Chaetopeltidaceae	Protosiphonaceae	Protosiphonaceae
Chlorococcineae	Oocystaceae	Scenedesmaceae
Planosporaceae	Hydrodictyaceae	Hydrodictyaceae
Hydrodictyaceae	Coelastraceae	
Ulotrichales (Isokontae)	Chlorosphaeraceae	Ulotrichales
	Chaetophorales	
Ulotrichaceae	Ulotrichaceae	Ulotrichaceae
Microsporaceae	Cylindrocapsaceae	Cylindrocapsaceae
Cylindrocapsaceae	Ulvaceae	Ulvaceae
	Blastosporaceae	Prasiolaceae
Chaetophoraceae	Chaetophoraceae	Chaetophoraceae
Aphanochaetaceae	Aphanochaetaceae	Aphanochaetaceae
Trentepohliaceae	Trentepohliaceae	Trentepohliaceae
Coleochaetaceae	Coleochaetaceae	Coleochaetaceae
	Chaetopeltidaceae	
Ulvaes (Isokontae)		
Ulvaceae		
Schizogoniales (Isokontae)		
Prasiolaceae		
Oedogoniales (Stephanokontae)	Oedogoniaceae	Oedogoniaceae

EMS OF CLASSIFICATION OF THE GREEN ALGAE  
(necessarily that of the respective authors)

Smith, 1933, 1938	Fritsch, 1935	Pascher, 1931 <sup>4</sup>
Volvocales	Volvocales	Volvocineae
Polyblepharidaceae	Chlamydomonadineae	Chlamydomonadales
Chlamydomonadaceae	Polyblepharidaceae	Polyblepharidaceae
	Chlamydomonadaceae	Chlamydomonadaceae, etc.
Phacotaceae	Phacotaceae	
Sphaerellaceae	Sphaerellaceae	Volvocales
Volvocaceae		Goniaceae
Spondylomoraceae		Volvocaceae, etc.
Tetrasporales	Tetrasporineae	Tetrasporinae
Coccomyxaceae		Tetrasporales
Palmellaceae	Palmellaceae	Palmellaceae
Tetrasporaceae	Tetrasporaceae	Tetrasporaceae
	Chlorodendrineae	Chlorangiales
Chlorangiaceae	Chlorodendraceae	Chlorangiaceae
		Hormotilaceae
Chlorococcales	Chlorococcales	Protococcineae <sup>5</sup>
Chlorococcaceae	Chlorococcaceae	Protococcaceae
Endosphaeraceae	Eremosphaeraceae	Eremosphaeraceae
Characiaceae	Chlorellaceae	Chlorellaceae
Protosiphonaceae	Selenastraceae	Protosiphonaceae
Scenedesmaceae	Dictyosphaeriaceae	Scenedesmaceae
Oocystaceae	Oocystaceae	Oocystaceae
Hydrodictyaceae	Hydrodictyaceae	Hydrodictyaceae, etc.
Coelastraceae	Coelastraceae	
Ulotrichales	Ulotrichales	Ulotrichineae
Ulotrichaceae	Ulotrichineae	Ulotrichinae
Microsporaceae	Ulotrichaceae	Ulotrichales <sup>6</sup>
Cylindrocapsaceae	Microsporaceae	Ulotrichaceae
	Cylindrocapsaceae	Cylindrocapsaceae
	Ulvaceae	Ulvaceae
	Prasiolineae	
	Prasiolaceae	Blastosporaceae
	Sphaeropleineae	
	Sphaeropleaceae	Chaetophorales
Chaetophoraceae	Chaetophorales	Microthamniaceae
	Chaetophoraceae	Chaetophoraceae
Trentepohliaceae	Trentepohliaceae	Aphanochaetaceae
Coleochaetaceae	Coleochaetaceae	Trentepohliaceae
	Chaetosphaeridiaceae	Coleochaetaceae
Protococcaceae	Pleurococcaceae	Chaetopeltidaceae
Ulvaes		Microsporinae
Ulvaceae		Microsporales
Schizomeridaceae		Microsporaceae
Schizogoniales		
Cladophorales	Cladophorales	
Cladophoraceae	Cladophoraceae	
Sphaeropleaceae		
Oedogoniales	Oedogoniales	Oedogoniineae
Oedogoniaceae	Oedogoniaceae	Oedogoniales
		Oedogoniaceae



West, 1916	Printz, 1927	Oltmanns, 1922
Siphonales (Isokontae)	Siphonales	Siphonales
Protosiphonaceae		
Bryopsidaceae	Bryopsidaceae	Bryopsidaceae
Caulerpaceae	Caulerpaceae	Caulerpaceae
Derbesiaceae	Derbesiaceae	Derbesiaceae
Codiaceae	Codiaceae	Codiaceae
Phyllosiphonaceae	Phyllosiphonaceae	
Vaucheriaceae	Vaucheriaceae	Vaucheriaceae
Chaetosiphonaceae		
Siphonocladales (Isokontae)	Siphonocladales	Siphonocladales
Cladophoraceae	Cladophoraceae	Cladophoraceae
Sphaeropleaceae	Sphaeropleaceae	Sphaeropleaceae
		Siphonocladaceae
Valoniaceae	Valoniaceae	Valoniaceae
Dasycladaceae	Dasycladaceae	Dasycladaceae
Conjugatae (Akontae)	Conjugatae	Conjugatae
Desmidiaceae	Desmidiaceae	Mesotaeniaceae
Saccodermæ	Saccodermæ	
Placodermæ	Placodermæ	Zygnemataceae
Zygnemataceae	Zygnemataceae	
	Charophyta	Desmidiaceae Charales

sedentary habit which is dominant among plants, and for that reason the coccoid forms are best referred to separate orders.

The great diversity exhibited among the coccoid green algae has led to the establishment of a large number of genera whose exact interrelationships are difficult to trace, especially as our knowledge of the life-history of many of them is still meagre. As a consequence no two authorities are agreed as to their classification into families, but little purpose would be served by discussing the different schemes here. In all series of coccoid forms (96), and very noticeably among Chlorophyceae, a more or less appreciable number seem to have completely abandoned the flagellate condition so that the daughter individuals never pass through a motile phase and acquire their mature characteristics before liberation from the membrane of the parent (so-called autospore formation). Brunnthaler (18) first utilised this feature in the classification of the Chlorococcales by subdividing the order into Zoosporinae and Autosporinae, according as reproduction was effected with the aid of zoospores (or motile gametes) or not. Oltmanns (92) and others

<sup>4</sup> Supplemented in parts from the "Süsswasserflora".

<sup>5</sup> After Brunnthaler (19).

<sup>6</sup> After Heering (55).

Smith, 1933, 1938	Fritsch, 1935	Pascher, 1931 <sup>4</sup>
Siphonales	Siphonales	Siphonineae
Halicystaceae	Protosiphonaceae	Monosiphonae
Bryopsidaceae		Valoniales
Caulerpacaeae	Caulerpacaeae	Caulerpales
Derbesiaceae	Derbesiaceae	
Codiaceae	Codiaceae	
Phyllosiphonaceae	Phyllosiphonaceae	Vaucheriales
Vaucheriaceae	Vaucheriaceae	Plectenchymatae
	Chaetosiphonaceae	Codiales
Siphonocladales		Siphonocladineae
		Radiatae
		Siphonocladales
		Dasycladales
		Cladophorinae
Valoniaceae	Valoniaceae	Cladophorales
Dasycladaceae	Dasycladaceae	Sphaeropleinae
Zygnematales	Conjugales	Conjugatae
	Euconjugatae	Saccodermiae
	Mesotaenioideae	Mesotaeniales
Mesotaeniaceae	Mesotaeniaceae	
	Zygnemoideae	Zygnemales
Zygnemataceae	Zygnemataceae	
	Mougeotiaceae	
	Gonatozygaceae	
	Desmidioidae	
Desmidiaceae	Desmidiaceae	Placodermiae
Charophyceae	Charales	Charophyta

have accepted this as the basis of classification among Chlorococcales, but, although it is convenient from a taxonomic standpoint, it may be questioned whether it affords a natural grouping. The step from the zoosporic to the autosporic condition may be induced by a change of environment; thus, the zoosporic *Chlorococcum* in cultures often multiplies without intervention of zoospores, while those forms of the zoosporic *Trebouxia* that constitute the algal partners of lichens likewise propagate by formation of autospores (aplanospores). The autosporic condition may well have originated in various evolutionary series among the coccoid green algae, and their segregation into Zoosporinae and Autosporinae probably obscures the actual affinities (*cf.* also 135, 465). In particular there is reason to suspect that the coenobial members of these two series (Hydrodictyaceae, Coelastraceae comprising forms like *Coelastrum*, *Scenedesmus*, etc.) are more closely interrelated than their reference to two suborders would imply. Moreover, in other classes (Xanthophyceae, Dinophyceae) a comparable separation of zoosporic and autosporic forms has proved to be altogether impractic-

cable. It is probable, therefore, that with increasing knowledge of details of reproduction a different grouping of Chlorococcales will be adopted.

#### CLASSIFICATION OF THE REMAINING CHLOROPHYCEAE

At the time when the importance of the Flagellata as a phase in algal evolution was first recognised, several attempts were made to separate other series from the large remaining mass of the Chlorophyceae. Bohlin (14, 25) grouped the Oedogoniales as Stephanokontae, implying an origin for these forms from a flagellate stock with a ring of flagella, although he retained the Stephanokontae as a subdivision of Chlorophyceae. Blackman and Tansley (8, 44), however, grouped them as a separate class (*cf.* also 161), and the same procedure was adopted with respect to the Conjugatae (Conjugales) which were named Akontae (8, 45). Diverse of the earlier authorities (90, 165) separated the Conjugatae from the remaining Chlorophyceae. Adoption of the classes Stephanokontae and Akontae was challenged by Fritsch (37, 38) on the grounds that their separation from other Chlorophyceae "must obscure the essential principles underlying the present-day concept of algal evolution, since in the pigmentation of their chloroplasts, in the possession of pyrenoids with a 'starch-sheath', in the storage of starch, and the chemical nature of their cell-walls, these two groups are altogether like other Chlorophyceae". In recent systems of classification (41; 100, 19; 135; 162) the classes Stephanokontae and Akontae have been abandoned and the two sets are grouped in the orders Oedogoniales and Conjugatae or Conjugales (Zygnematales of Smith) among Chlorophyceae. Oltmanns (92) and Printz (113), however, still subdivide the green algae into two main divisions, the Euchlorophyceae and Conjugatae of the latter. The Conjugatae show many peculiarities, but they can hardly be regarded as exhibiting a greater measure of distinguishing characteristics than do the Oedogoniales or Siphonales, and it may be doubted that the attitude of Oltmanns and Printz is justified. In Oltmanns' treatment the diatoms are interposed between consideration of the Conjugatae and that of the remaining Chlorophyceae, but, despite a certain degree of parallelism, this juxtaposition of Conjugales and Bacillariales is quite unwarranted, since there can be no affinity between these two groups.



The Chlorophyceae comprise a larger number of filamentous and simple thalloid forms than are to be met with in any other class of algae, and marked differences of opinion have arisen as to their grouping. The writer (41, 73) recognises, apart from Oedogoniales and Conjugales, only three orders of filamentous Chlorophyceae—Ulotrichales, Cladophorales, Chaetophorales. All other authorities include the Chaetophorales in the Ulotrichales, called Chaetophorales by Wille (166) and Printz (113), although the numerous genera comprised in Fritsch's Chaetophorales are invariably placed in families (Chaetophoraceae, Trentepohliaceae, *etc.*) distinct from those harbouring the true Ulotrichales. Reference of the former to a separate order by the writer turns on the recognition of the great phylogenetic importance of their special habit which has been designated as heterotrichous (38, 111). In typical representatives of Chaetophorales (*Stigeoclonium*, *Trentepohlia*, *Coleochaete pulvinata*) the plant body is developed as two distinct systems, a primarily formed prostrate one and a secondarily formed erect one. An altogether comparable differentiation of the plant body is met with in the simpler filamentous brown and red algae and is also recognisable among blue-green algae (42, 44). The Chaetophorales are in fact in vegetative habit parallel to the simpler members of Ectocarpales and Nemalionales among Phaeophyceae and Florideae, respectively, while forms parallel to the Ulotrichales are not found in these orders. Among Phaeophyceae and Rhodophyceae many of the more specialised forms pass through a primary heterotrichous stage, and it is evident that this habit has afforded an important starting point for the development of larger and more highly differentiated types of algal thalli.

While the families Chaetophoraceae, Trentepohliaceae and Coleochaetaceae are in general well defined, a group of aquatic genera (*Gongrosira*, *Ctenocladus*, *etc.*), commonly classed as Gongrosireae (Leptosireae of Printz (113)), as well as the endophytic and usually lime-boring Gomontieae, are difficult to place. Smith (135) and Fritsch (41, 280) class them among Trentepohliaceae, an otherwise essentially terrestrial group; this was the practice at first adopted (165) but later (166) abandoned by Wille. Both he and Printz (113) include the Gongrosireae and Gomontieae in the Chaetophoraceae (*cf.* also 161). As compared with the typical members of the latter, the Gongrosireae and Gomontieae are distin-

guished by an absence of hairs and more especially by a usual differentiation of distinct sporangia. They afford evidence of a greater degree of specialisation and in various respects certainly approach more closely to the terrestrial Trentepohlieae. It might be better until such time as they have been more fully studied to place them in a separate family.

As in other heterotrichous series, the Chaetophorales comprise a considerable number of reduced and in part unicellular forms (*Chaetosphaeridium*, *Dicranochaete*, etc.) whose exact affinities are, in the present state of our knowledge, difficult to assess. They are usually grouped in a single family, the Chaetosphaeridiaceae of Fritsch (41), although this constitutes an altogether artificial assemblage of forms. Smith's (135, 411) reference of them to Coleochaetaceae can scarcely be justified, while West's (161) inclusion of them among Protococcales obscures their undoubted affinities with Chaetophorales. West (cf. also 113) classes them with *Chaetopeltis* as Chaetopeltidaceae, but, although the genus *Chaetopeltis* possibly includes types that should be referred to Chlorococcales (70), the *Chaetopeltis* of Berthold (5) is no doubt a member of Chaetophoraceae (41, 260; 135, 402; 22). *Pleurococcus* (*Protococcus*) is now generally recognised as an extremely reduced genus, possibly related to some of the Trentepohlieae.

Wille (165), Oltmanns (92) and Printz (113) group all filamentous Chlorophyceae, including the Oedogoniaceae but excluding the Zygnemales and Cladophoraceae, in one comprehensive order, variously styled Chaetophorales or Ulotrichales (cf. also 104). Setchell and Gardner (131) and Smith (135), on the other hand, segregate from the Ulotrichales, apart from the Oedogoniales, the two orders Ulvales and Schizogoniales, the former first distinguished by Blackman and Tansley (8), the latter first established by G. S. West (159; cf. also 20). Reference of the forms comprised in these two series to separate orders is a matter of opinion. The Ulvaceae undoubtedly show a vegetative advance over other Ulotrichales, and they differ also in the possession of an isomorphic life-cycle. On the other hand, the early stages of *Ulva* and *Enteromorpha* are filamentous, and such stages, especially in the latter, closely resemble *Ulothrix*; moreover, there is great resemblance in details of reproduction. Smith (135, 457; cf. also 67) refers to the Ulvales, also a family Schizomeridaceae, in which he includes the

genus *Schizomeris*, an alga of doubtful status which many have regarded but as a developmental state of *Ulothrix* (cf. 41, 201). Fritsch (41) classes the Ulvaceae in the suborder Ulotrichineae side by side with the Ulotrichaceae (cf. also 149) to which he refers *Schizomeris*.

A better case can be made out for referring the Prasiolaceae (Blastosporaceae of Printz (113) and Heering (55)) to the separate order Schizogoniales (Prasiolales (65, 149)). In the possession of an axile chloroplast and the apparent absence of motile stages during reproduction, which is largely vegetative, they stand markedly apart from other Ulotrichales. Forms with an axile chloroplast are known among coccoid (*Trebouxia*) and palmelloid (*Asterococcus*) green algae, although in them multiplication is effected by motile elements; moreover, certain species of *Chlamydomonas* have axile chloroplasts (103), although these are rather different in type from those of the other green algae mentioned. It may be that better knowledge of Prasiolaceae will lead to recognition of a definite evolutionary series among Chlorophyceae comprising forms with axile chloroplasts, and there is a remote possibility that the Conjugales in which the chloroplasts are predominantly axile and reproduction by motile elements is lacking, might be connected with this line. Fritsch (41) includes the Prasiolaceae in the suborder Prasiolineae among Ulotrichales.

Bohlin (14, 25) referred the genus *Microspora*, distinguished by its walls being composed of H-shaped pieces as in *Tribonema* and diverse other Xanthophyceae, as well as by the absence of pyrenoids, to a distinct order, but most recent authorities accept a near relation to the Ulotrichaceae. Pascher (104, 327), however, places *Microspora* in a separate division (Microsporineae) of his Ulotrichineae (cf. also 55, 146) and suggests a possible relationship to certain Chlorococcales with a cell wall composed of two pieces.

Many systematists recognise two orders of siphonous green algae, the Siphonales and the Siphonocladales (92, 100, 113, 131, 135, 161, 166), although Blackman and Tansley (8) grouped them as two suborders (Siphoneae, Siphonocladeae) in the single order Siphonales. The Siphonocladales<sup>7</sup> comprise numerous genera in

<sup>7</sup> Most of those who recognise the order Siphonocladales include the Dasycladaceae in it. The origin of this peculiar error is obscure. In *Dasycladus*, *Cymopolia*, *Acetabularia*, etc. the body is one continuous coenocyte and no septation of any kind is recognisable in the vegetative region.



which the mature thallus consists of few or many multinucleate segments, and to them most authorities refer the Sphaeropleaceae and the Cladophoraceae. Fritsch (162, 151) was the first to depart from this practice, the two families last mentioned being referred to separate suborders of the Ulotrichales (*cf.* also 135), while subsequently (41) the Cladophoraceae were placed in a distinct order, the Cladophorales. Such an order is likewise recognised by Smith (136), although he includes in it also the Sphaeropleaceae. Pascher (104, 328, footnote) points out that the Cladophoraceae and Sphaeropleaceae are probably not related to the main series of the Siphonocladales and that they are likely to have quite a different affinity.

The reference by Fritsch of the genus *Sphaeroplea* to the suborder Sphaeropleineae of Ulotrichales is based on a survey of all its morphological features (39). Relevant are (*a*) the annular chloroplasts, closely resembling those of *Ulothrix zonata*, although more complex reticulate types develop in certain species in later stages, (*b*) formation of the sexual cells (ova and spermatozooids) in the ordinary segments of the filaments, (*c*) liberation and reception of the male cells through small apertures in the wall, one commonly situated near each point of occurrence of a primary annular chloroplast unit, and (*d*) the haploid life-cycle. *Sphaeroplea* is regarded as an advanced *Ulothrix*-like type in which septation is retrogressive. There is some indication, moreover, that there may exist sphaeropleaceous types which have not attained the oogamy exhibited by the ordinary species (*Sphaeroplea tenuis* (39, 18)). It is difficult to detect any affinities to Cladophoraceae.

The members of this family are unbranched (*Urospora*, *Chaetomorpha*) or richly branched (*Cladophora*) filamentous types, many of which appear to have advanced to an isomorphic life-cycle. The usually large cells contain numerous nuclei and an often complex reticulate chloroplast which, in certain species, apparently later fragments into many separate pieces, often still retaining the primary reticulate arrangement. The young plants are filamentous from the first and the germ-lings formed by zoospores and zygotes undergo progressive septation by cross walls which arise as annular ingrowths from the longitudinal walls (17). Zoospores and gametes are formed in large numbers in the ordinary vegetative cells and are liberated through a lateral aperture, as in *Ulothrix*. Germ-

lings of *Urospora* have a curved plate-like parietal chloroplast, closely resembling that of Ulotrichaceae and Ulvaceae, and the young cells harbour but few nuclei (114, 280). The cells of some species of *Rhizoclonium* permanently possess only a few nuclei (110). For these diverse reasons the Cladophorales are regarded as filamentous types in which elaboration of the cells and appearance of a coenocytic character is secondary. They may have originated from a ulotrichaceous stock.

After removal of the Sphaeropleaceae and Cladophoraceae there remain among Siphonocladales a large number of marine genera which are commonly referred to a number of separate families (11, 18); certain of them (*Cladophoropsis*, *Boodlea*) exhibit considerable superficial resemblance to *Cladophora*. There are, however, marked points of difference. The germlings are vesicular, and more or less closely resemble *Valonia* which is usually regarded as the most unspecialised member of this series. The division into multinucleate segments is accomplished, moreover, in an entirely different manner by a process styled "segregative division" by Boergesen (10, 34). The protoplasm of the coenocyte contracts and undergoes simultaneous division into a number of multinucleate masses, each of which becomes surrounded by a membrane independent of that of the parent coenocyte. Subsequently the segments enlarge and become pressed against one another so that the double membranes delimiting them may be difficult to recognise; the segments may again divide in the same manner. In various genera (*Siphonocladus* (9), *Cladophoropsis*, etc.) the segments tend to assume a linear arrangement, and some of them grow out as branches, giving the cladophoraceous habit referred to above. Segregative division has been established for *Valonia*, *Dictyosphaeria*, *Siphonocladus*, *Cladophoropsis* and *Struwea*, besides others, but it has not been shown to occur in *Microdictyon* and *Anadyomene*. It has recently been found (58, 59) that these two genera possess an isomorphic life-cycle, the diploid phase producing quadriflagellate zoospores and the haploid biflagellate isogametes. The type of life-cycle, contrasting so markedly with the diploid one now established for a considerable number of Siphonales (including *Valonia* (126)), raises the question whether these two genera are correctly associated with the other segmented Siphonales (43, 537), and it is possible that they should be referred to Cladophorales.

However that may be, it is difficult to find any clear indications of affinity between the other Siphonocladales and the Cladophorales. Fritsch (41, 424) has suggested that segregative division may be interpreted as a process of cyst-formation in which the cysts are retained and germinate *in situ*. On this view the series of genera exhibiting this mode of segmentation can be regarded as variously developed colonial types, in which the unit is a coenocyte. The peculiar process of segregative division represents one of the many diverse ways in which the siphonous green algae have evolved into larger thalli with considerable mechanical stability. The writer can recognise no reasons for placing the genera under discussion in a separate order and is of the opinion that they should be included in one or more families among Siphonales.

Feldmann (33) has opposed removal of the Cladophoraceae from the segmented Siphonales, but this is not the place to enter into a detailed discussion of his position, with which the writer will deal elsewhere. The chloroplast characters upon which he lays particular stress can be regarded only as of subsidiary importance.

The Vaucheriaceae, the only known oogamous Siphonales, have been a source of much perplexity to systematists. *Vaucheria* has been suspected of being a member of Xanthophyceae, and the Vaucheriaceae were indeed placed in that class by Blackman and Tansley (8, 58). This was based mainly on the occurrence of oil as the photosynthetic product, which has been stated (12, 30; 113, 328) to go hand in hand with the presence of an excess of xanthophyll in the chloroplasts, and on the mode of arrangement of the flagella on the spermatozoids, which is unlike that characteristic of Chlorophyceae. Pascher (56, 69, footnote) also suspects inequality of the pairs of flagella on the compound zoospore. Except for the presence of oil, all these characters are of dubious value for assigning to *Vaucheria* a position among Xanthophyceae. The presence of excess xanthophyll has never been adequately proved and the arrangement of the flagella on the spermatozoids is as little typical of the Xanthophyceae as it is of Chlorophyceae. Discovery of the starch-producing *Dichotomosiphon* (31), with sex organs comparable in type to those of *Vaucheria*, went far to establish a chlorophycean affinity for the two genera and, in view of the vegetative resemblances between *Dichotomosiphon* and the filaments of Codiaceae, to support an inclusion among Siphonales. The genera



*Vaucheriopsis* and *Pseudodichotomosiphon* (41, 428)), established during the last 20 years, have not helped in the elucidation of affinities. Dangeard's (26, 184) discovery of the presence of pyrenoids in certain marine species of *Vaucheria* is also of no assistance in this connection, since such structures occur also in some Xanthophyceae.

The possibility that the resemblances between *Vaucheria* and *Dichotomosiphon* may be homoplastic must be envisaged, and the true affinities of the former can not be held conclusively proved until a more detailed study of zoospores and spermatozoids has been undertaken and the proportions of the chloroplast pigments adequately established. It is now almost a platitude to point out that nearly all oogamous green algae occupy very isolated positions, which renders elucidation of their affinities a matter of considerable difficulty.

The status of the Conjugales (Zygnematales of Smith) has already been considered. Detailed classification of the filamentous members presents considerable difficulties, but can not profitably be discussed here. Desmids, comprising a wide diversity of unicellular and colonial types, have long been classed in the two series Saccodermæ and Placodermæ, the latter including the great bulk of the species. The Saccodermæ possess a simple cell wall of a single piece and in general exhibit less specialised types of chloroplasts than the Placodermæ, where the wall consists of two overlapping pieces and is perforated by numerous pores. While earlier authorities (87; cf. also 113, 161) accepted the two series of desmids as closely allied, Oltmanns (90, 53) first emphasised the probable primitive character of the Saccodermæ (his Mesotaeniaceae), which he regarded as most closely related to the ancestral type from which the Placodermæ and filamentous Conjugales were supposed to have diverged as separate lines. In adopting this position he laid stress on the fact that several genera of Mesotaeniaceae (*Mesotaenium*, *Cylindrocystis*) produce four individuals from their zygotes, while in Placodermæ there are usually two and in filamentous Conjugales only one, the supernumerary nuclei aborting. Later researches have shown that these numbers are not invariable and that there are also Placodermæ producing four individuals from the zygote (153), while two are occasionally formed in *Mesotaenium* (146, 160) and *Spirotaenia* (61, 765), and this ap-

pears to be the rule in *Netrium* (111, 669). There is evidence of a fairly close affinity between the Saccodermæ and the filamentous forms, but the relation of the highly specialised Placodermæ to the others is not clear; in particular, their complex wall structure separates them sharply from the other two series. The writer (41) has therefore grouped the Conjugales in two suborders, Euconjugatae and Desmidioidae, distinguishing among the former the two series Mesotaenioideae and Zygnemoidae. Pascher (104) has adopted a similar grouping (*cf.* also 25, 32).

Oltmanns (90, 52) was also the first to separate the genera *Gonatozygon* and *Genicularia* from the desmids and to interpret them as filamentous members with a marked tendency to fragment into individual cells. As in other filamentous Conjugales, only a single individual is formed from the zygote. Fritsch (41) follows Oltmanns and refers these genera to the family Gonatozygaceae of Zygnemoidae. Smith (135), on the other hand, retains *Gonatozygon* and *Genicularia* among Mesotaeniaceae. So far no basis has been found for classing the Placodermæ in more than one family, and indeed the limits of many genera are so ill defined (40) that it is unlikely that any such grouping could be achieved.

The Characeae, which have a more highly differentiated vegetative system than is found in the multicellular Chlorophyceae and possess highly complex sex organs, are regarded by most as belonging to a separate class of algae (Charophyceae (135)) or even to a separate subdivision of the vegetable kingdom (Charophyta). Fritsch (41), on the other hand, groups them as an order of Chlorophyceae (Charales). The attitude taken depends on the particular characteristics that are stressed, but it is well to realise that there is no evidence that the Characeae differ from the Chlorophyceae either in the nature and proportions of their photosynthetic pigments or in their metabolism; the spermatozoids, though highly specialised, are, moreover, isokontan in type and the life-cycle is haploid.

#### CLASSIFICATION OF THE PHAEOPHYCEAE

During the early part of the present century the classification of this class initiated by Kjellman (63) in the "Natürliche Pflanzenfamilien" dominated the outlook. Oltmanns (90, 348; 91, 19), following him, grouped the brown algae into (*a*) Phaeosporeae (150, 216), propagating by zoospores and sometimes by motile gametes;

(b) Acinetosporeae, distinguished by usual propagation by large motionless monospores; and (c) Cyclosporeae, characterised by oogamous reproduction. The first of these subdivisions included the numerous diverse forms comprised in the so-called Ectocarpaceae, as well as the Cutleriaceae, the Sphacelariaceae and Laminariaceae, the second the Tilopteridaceae, and the third the Fucaaceae and Dictyotaceae, although Kjellman (63), unlike later authors, excluded the Dictyotaceae from the Phaeophyceae. A similar arrangement was adopted by Setchell and Gardner (132), although they substituted the name Aplanosporeae for the Acinetosporeae of Oltmanns and included in this group, characterised by possession of motionless asexual reproductive cells, both Tilopteridaceae and Dictyotaceae.

The rapid strides in the elucidation of the life-cycles of Laminariaceae and subsequently of diverse genera of Ectocarpales during the second and third decades of this century showed that oogamous sexual reproduction was more widespread than had hitherto been supposed and rendered Kjellman's grouping untenable. A new classification of the class into a number of orders of equal rank was proposed by Kylin (74, 308) and adopted with considerable amplifications by Oltmanns (93) in the second edition of his book. The latter recognised seven orders: Ectocarpales, Sphacelariales, Cutleriales, Laminariales, Tilopteridales, Dictyotales and Fucales. With the exception of the first, these main subdivisions have been retained by later authorities.

Sauvageau's demonstration (119) that *Dictyosiphon* possesses a heteromorphic life-cycle, the zoospores produced in its unilocular sporangia producing minute filamentous gametophytes propagating by isogametes, afforded a new character for the subdivision of the large and unwieldy group of the Ectocarps, from which the Cutleriaceae had already been removed by Oltmanns (93). Taylor (147) proposed reference of the Dictyosiphonaceae to a separate order, Dictyosiphonales (cf. also 144), while a few years later Sauvageau (120) referred the Sporochneaceae, in which he had established a heteromorphic alternation analogous to that of Dictyosiphonaceae, though seemingly with oogamous reproduction of the gametophyte, to a distinct order, the Sporochneales.

More recently still, Kylin (80, 91; cf. also 148) has grouped the bulk of the Phaeophyceae into Isogeneratae with isomorphic, and



Heterogeneratae with heteromorphic alternation, and distinguishes in each of these main subdivisions a number of orders. Among Isogeneratae he includes the Ectocarpales (*sens. limit.*), Sphacelariales, Cutleriales, Tilopteridales and Dictyotales, among Heterogeneratae the Laminariales, Sporochnales, Desmarestiales, Chordariales, Dictyosiphonales and Punctariales; the last three, all with isogamous sexual reproduction and included in Oltmanns' Ectocarpales, are distinguished only by vegetative characteristics. Sporochnales and Desmarestiales, likewise classed in Ectocarpales by Oltmanns, have gametophytes with oogamous sexual reproduction. The Fucales, in which a true phase-alternation is lacking, constitute a third subdivision of Phaeophyceae (Cyclosporeae) in Kylin's scheme. This classification is adopted by Taylor (149) and G. M. Smith (136).

Kylin's order Ectocarpales is restricted to those members of Oltmanns' order that show isomorphic alternation, namely, the filamentous Ectocarpaceae and some of the Myrionemataceae (*Nemoderma*, *Lithoderma*). Certain genera at present usually included in the latter family appear to be heteromorphic, and are regarded by Kylin as probably reduced Mesogloeaceae (his Chordariaceae, order Chordariales), which may well be so. The writer (43, 545) has given considerable evidence for the view that the heteromorphic life cycle prevalent among the majority of the more specialised genera belonging to the Ectocarpales of Oltmanns is derived, by divergent development of the two generations, from an isomorphic alternation, comparable to that exhibited by the Ectocarpaceae. The same interpretation is advanced for the origin of the heteromorphic life-cycle of *Cutleria* (42, 409), and since Kylin refers the Cutleriales to his Isogeneratae, he evidently holds the same view. If, however, such a markedly heteromorphic type as *Cutleria* is associated with the isomorphic *Zanardinia*, with which it is no doubt closely allied, in the same order of Isogeneratae, then the heteromorphic Chordariales, Dictyosiphonales and Punctariales should also be included with Kylin's Ectocarpales in a common order, since their heteromorphic life cycle is just as clearly derived from an isomorphic one as is that of *Cutleria*. Moreover, there is considerable evidence (1; 2; 132, 550) that the Pacific genus *Heterochordaria*, which in vegetative structure approximates sufficiently to *Chordaria* to have been formerly included

in that genus, possesses an isomorphic life cycle. In other words, it seems that this type of life cycle is not altogether confined to the filamentous Ectocarpaceae and the crust-forming Myrionemataceae, but exists also among some of the more highly elaborated types which on the basis of their vegetative structure would be included in Kylin's Chordariales.

The genera of Chordariales, Dictyosiphonales and Punctariales share with the Ectocarpales an essentially isogamous sexual reproduction and the heterotichous habit that is invariably displayed during early stages of development in the sporophyte (42, 402); as regards the Punctariales, too, there is a close linkage with the filamentous Ectocarpaceae by way of such genera as *Phloeospora* and *Isthmoploea*. For these various reasons the writer in the second volume of his book "The Structure and Reproduction of the Algae" has adopted the more comprehensive conception of the Ectocarpales taken by Oltmanns, although segregating from them the oogamous Sporochneaceae and Demarestiaceae (*cf.* also 45, 53). He recognises nine orders of Phaeophyceae: Ectocarpales, Tilopteridales, Cutleriales, Sporochneales, Desmarestiales, Laminariales, Sphacelariales, Dictyotales and Fucales.

Kylin's Chordariales comprise a large proportion of the haplostichous Ectocarpales of Kuckuck (71), while Dictyosiphonales and Punctariales are the polystichous Ectocarpales of the same authority. The limits of the Chordariales are indicated in the valuable survey recently published by Kylin (82), in which a progressive restriction of meristematic activity, culminating in the Spermatochneaceae with apical growth, is described. The only essential difference between Dictyosiphonales and Punctariales lies in the more or less clearly marked apical growth of the former, and it is not improbable that they may possess the same relation to the Punctariales as the Spermatochneaceae do to other Chordariales. The objection to the recognition of any of these as separate orders is that it obscures their close relation to other Ectocarpales; moreover, the differences between them and the latter are not of the nature usually accepted for distinguishing major systematic units.

It would be going too far to consider the detailed grouping of the genera of Ectocarpales (*sens. lat.*). There is rather general agreement about the limits of many families recognised at present<sup>8</sup>,

<sup>8</sup> Such are: Ectocarpaceae, Myrionemataceae, Elachistaceae, Mesogloeoceae (Chordariaceae), Acrotrichaceae, Spermatochneaceae, Punctariaceae, Asperococcaceae, apart from the polystichous families referred to above.

and the chief differences of opinion are encountered in relation to the grouping of the polystichous (parenchymatous) forms where relatively few serviceable systematic characters are now available. All authorities recognise the family Dictyosiphonaceae, and most have accepted the family Encoeliaceae established by Oltmanns (93) for a diversity of parenchymatous genera (*Soranthera*, *Colpomenia*, *Chnoospora*) whose only other common characteristic is the production of sporangia around groups of hairs which are often sunk in a depression of the thallus surface. Although this family is almost certainly artificial (*cf.* especially 121, 326), no more satisfactory basis of classification has so far been found (*cf.* however, 132, 522).

Exclusion of Cutleriales, Sporochnales and Desmarestiales from the Ectocarpales is warranted not only in possession by the members of each order of a distinctive vegetative organisation and of marked specialisation in reproduction, but also by elimination of the early heterotrichous stages that are so characteristic of Ectocarpales. The marked oogamy of *Desmarestia* and the far-going resemblances between its gametophytes and those of Laminariales, led Schreiber (125), who first elucidated these matters, to propose an inclusion of Desmarestiaceae in Laminariales, but this has rightly not been followed since in vegetative characteristics there are very profound contrasts between the two orders. The uniformity in general organisation among the members of Sphacelariales has long led to their recognition as a coherent unit among Phaeophyceae. Classification of the order into Sphacelariaceae, Stypocaulaceae and Cladostephaceae by Oltmanns (93), on the basis of Sauvageau's comprehensive studies (118), has been generally accepted. Nor are there any differences of opinion about the limits of the Dictyotales.

Discovery of the gametophytes of *Chorda* resulted in transference of this genus from the Ectocarpales, among which it was formerly classed, to the Laminariales, where it occupies a family of its own (Chordaceae) on the grounds of its simple vegetative structure. The remaining Laminariales are now usually grouped in the three families Laminariaceae, Lessoniaceae and Alariaceae, established by Setchell (129). The diverse taxonomic series distinguished by Oltmanns among Fucales (89, 93) have been given the rank of families by the writer in his forthcoming book (46); he dis-

tinguishes Fucaceae (*Fucus*, *Pelvetia*, *Ascophyllum*, *Seirococcus*, etc.), Himanthaliaceae (*Himanthalia*), Cystoseiraceae (*Pycnophycus*, *Halidrys*, *Cystoseira*, etc.), Sargassaceae (*Sargassum*, *Coccolophora*, etc.), Hormosiraceae (*Notheia*, *Hormosira*), Durvilleaceae (*Durvillea*) and Ascoseiraceae (*Ascoseira*). The last of these (134, 50) awaits further investigation before its exact affinities can be determined, while the relation of the Durvilleaceae to the other families remains obscure. It may be mentioned here that the genus *Splachnidium*, often doubtfully included in the Fucales in the past, has now been shown (71, 133) to be a specialised member of the haplostichous Ectocarpales.

#### CLASSIFICATION OF THE RHODOPHYCEAE

A broad division of this class into Bangioideae (Bangiales) and Florideae has long been recognised (124). The principal distinctions are the lack of differentiated carpogonia and the direct division of the zygote into carposporangia in the former; features of lesser importance are the absence of pit-connections between the cells, diffuse growth and frequent presence of axile chromatophores in the Bangioideae. The latter are a small group comprising a number of marine filamentous (*Erythrotrichia*) and parenchymatous genera (*Bangia*, *Porphyra*), as well as a rather varied assortment of largely freshwater or terrestrial palmelloid types (*Asterocytis*, *Porphyridium*, *Chrootheca*) which are usually regarded as reduced forms. Rosenvinge (116, 56) grouped the genera as Bangieae, Erythrotrichieae and Goniotrichieae (cf. also 142), whilst the writer (46) recognises two families, Bangiaceae (with Bangieae and Erythrotrichieae) and Porphyridiaceae (with *Goniotrichum*, *Asterocytis*, *Porphyridium*, etc.) (cf. also 81, 39). In both families genera with one (*Kyliniella*, *Porphyropsis*) or more (*Rhodospira*) parietal chromatophores are known. It is possible that, as is true of some desmids (40), these are derivative forms in which the central part of the axile chromatophore typical for the members of this subclass has been suppressed, while its peripheral processes have become enlarged.

The relatively simple vegetative organisation, the simple sex organs, and the direct germination of the zygote led Rosenvinge (117) to regard the Bangioideae as primitive among Rhodophyceae and to suggest the name Protoflorideae for them, a name which has been adopted in a few quarters. It must be realised, however, that



the direction of vegetative development among the Bangiaceae is quite different from that among the Florideae. The former exhibit a marked parenchymatous tendency and possess diffuse growth, while the Florideae are pseudoparenchymatous uni- and multiaxial forms with apical growth. True, in both series the least specialised genera (*Erythrotrichia*, *Acrochaetium*) in part possess a heterotrichous filamentous habit (42, 399), but that is clearly a step in evolution that was reached in all classes of algae that passed beyond the simple filamentous stage. The exact degree of relationship between Bangioideae and Florideae is not at present clear, but, whatever it may amount to, it is unlikely that the two subclasses represent more than a divergent development in quite different directions from a common ancestry (cf. also 81, 55).

Among the many diverse genera included in Florideae, a distinction between those forming gonimoblast threads (which produce the carposporangia) directly from the carpogonia and those forming these threads from other adjacent or distant cells (auxiliary cells) after fertilisation was already recognised by Bornet and Thuret (15, 159) and more clearly stated by Schmitz (123). The genera showing the former feature (*Acrochaetium* = *Chantransia*, *Batrachospermum*, *Nemalion*, etc.) are classed in the order Nemalionales (124), the limits of which have become more sharply defined as a result of the demonstration by Svedelius in 1915 (143) that in *Scinaia* the first divisions in the germinating zygote are meiotic so that the gonimoblasts and carpospores contain the haploid number of chromosomes. This haplobiontic condition was subsequently established also in *Nemalion*, *Batrachospermum* and other members included in Nemalionales, while *Atractophora* and *Naccaria* (76, 11), *Bonnemaisonia* (72; 76, 21) and *Asparagopsis* (145), formerly classed in other orders of Florideae, were shown by Kylin and Svedelius to belong to Nemalionales.

This order in its present limits exhibits an appreciable range in vegetative construction from simple filamentous genera like *Acrochaetium* to relatively specialised uni- (*Bonnemaisonia*, *Asparagopsis*) and multiaxial (*Scinaia*) forms. Hand in hand with this, but not exactly parallel to it, goes an increasing complexity in the post-fertilisation events. Kylin (76, 114; 81, 57) consequently recognises a considerable number of families<sup>9</sup> differing in vegetative and

<sup>9</sup> *Acrochaetiaceae*, *Batrachospermaceae*, *Lemaneaceae*, *Naccariaceae*, *Bonnemaisoniaceae*, *Helminthocladiaceae*, *Chaetangiaceae*; of these, the last two comprise the multiaxial genera.

reproductive features. It is significant that in the more specialised uni- (Bonnemaisoniaceae) and multiaxial (Chaetangiaceae) families there is a tendency for the diploid nucleus, prior to meiosis, to pass into a cell underlying the carpogonium, for differentiation of special nutritive cells or threads in the neighbourhood of the latter, and for development of a sterile envelope around the gonimoblast. These are features met with in the other series, the diplobiontic Florideae considered below, and the facts imply that a pronounced evolutionary advance, parallel to some extent with that found among diplobiontic forms, has occurred also among the haplobiontic Nemalionales, and that the two large series of Florideae represent divergent developments from some common source. So far as present evidence goes, all Nemalionales pass through a typical heterotrichous stage during early development (43, 400).

Schmitz (124) recognised three main subdivisions among the remaining Florideae, the Cryptonemiales, Gigartinales and Rhodymeniales. These are all distinguished not only by the origin of the gonimoblasts from special auxiliary cells but also by possession of tetrasporangia, for the most part borne on distinct plants. It was first established by Yamanouchi (167) in *Polysiphonia* that in these Florideae the postfertilisation nuclear divisions in the zygote are not meiotic, that the carpospores are diploid, that this is also true of the vegetative cells of the plants bearing tetrasporangia, and that the reduction divisions ensue during formation of the four spores in the latter. Similar features were demonstrated in *Martensia* (140), *Griffithsia* (73, 83) and *Delesseria* (141), while Lewis (84) by direct cultures established the alternation between haploid sexual plants producing diploid carpospores and diploid asexual plants producing haploid tetraspores. Since then this kind of life-cycle, styled diplobiontic by Svedelius (143, 43), has been established for a considerable number of other genera belonging to the orders above mentioned.

The broad basis of classification among these diplobiontic Florideae still follows the lines laid down by Schmitz and depends essentially on the features of the reproductive process. Recent writers, following Kylin (76, 113; 77, 90; 81), distinguish Gelidiales, Cryptonemiales, Gigartinales, Rhodymeniales and Ceramiales. The order Ceramiales was first established by Oltmanns (90, 683). It includes the majority of Schmitz's Rhodymeniales and is dis-

tinguished from the remnant, still grouped as Rhodymeniales, by the invariable uniaxial construction and by the fact that auxiliary cells are cut off from special mother-cells only after fertilisation. The Rhodymeniales in their present delimitation include multi-axial forms in which the auxiliary cells of the procarps, although cut off before fertilisation, do not attain full differentiation until that process has occurred. A further difference emphasised by Fritsch (42, 400) is that in Rhodymeniales the germinating spore always divides by a number of walls perpendicular to the substratum to form an obscure prostrate system, prior to production of the erect growth, while in Ceramiales the first dividing walls in the spore are parallel to the substratum and growth is erect from the first.

The Gelidiaceae (*Gelidium*, *Pterocladia*, etc.), although possessing distinct tetrasporic individuals, resemble the less specialised Nemalionales, among which they were classed by Schmitz (124), and differ from other diplobiontic forms in the fact that the gonimoblasts arise directly from the carpogonia and that there are no auxiliary cells. There is reason to suspect a diplobiontic life-cycle, although this has not yet been cytologically established. Kylin's (75, 132; 76, 24) reference of these few genera to a separate order is, however, justified also on other grounds, *viz.*, the origin of the fruit from an aggregate of procarps (compound procarp of Kylin (76, 27)). Certain Nemalionales (a few species of *Acrochaetium*, *Galaxaura*) bear tetrasporangia on distinct individuals, and it is within the realms of possibility that further study may necessitate their removal to the diplobiontic Florideae, but since tetrasporangia in various other species of *Acrochaetium* occur on sexual individuals, commonly together with monosporangia (neutral sporangia (135, 115)), it is perhaps more probable that these tetrasporangia of Nemalionales merely represent monosporangia with divided contents and that they are not the seat of a reduction division (43, 550).

Whilst Nemalionales, Gelidiales, Rhodymeniales and Ceramiales constitute well defined groups, this is scarcely true of the other two orders at present recognised, the Cryptonemiales and Gigartinales, which include a large number of common Florideae. The only essential difference is that in Gigartinales (79, 72) the auxiliary cells are intercalary cells of the ordinary threads composing the

vegetative system, while in Cryptonemiales the auxiliary cells are situated in special accessory branches. Although this is a taxonomic distinction easily recognised, it can scarcely be supposed to afford the basis for a natural classification. Both orders include families (*e.g.*, Grateloupiaceae and Dumontiaceae among Cryptonemiales, Furcellariaceae and Solieriaceae among Gigartinales) in which carpogonia and auxiliary cells are produced on distinct branch-systems, often remote from one another, and others (*e.g.*, Gloeosiphoniaceae and Callymeniaceae among Cryptonemiales, Rhodophyllidaceae and Gigartinaceae among Gigartinales) in which they are approximated to form more or less clearly defined procarps; in the former there is a development of often elongate connecting threads by means of which the products of division of the diploid zygote nucleus are transferred to the auxiliary cells. Such differences will perhaps provide a more satisfactory basis for classification of these Florideae into two or more orders. The nemathecial habit (including the corallineaceous conceptacle) might afford another character that could be deemed to be of ordinal rank. At one time Kylin (76, 121; 77, 99) recognised a further order, the Nemastomales (including Rhodophyllidaceae, Sphaerococcaceae, Nemastomaceae), but this was subsequently (79) merged in the Gigartinales, when the basis of distinction was found to be unsatisfactory.

In the two orders Cryptonemiales and Gigartinales Kylin recognises numerous families<sup>10</sup>, distinguished *inter alia* by the features mentioned above, by the vegetative structure (uni- and multiaxial families), and by the mode of arrangement of the tetraspores (cruciate or zonate). The Rhodymeniales (78) are at present classed into Champiaceae and Rhodymeniaceae, of which the latter are not very clearly defined and possibly heterogeneous. The many diverse genera of Ceramiales have long been grouped in the three families Ceramiaceae, Delesseriaceae and Rhodomelaceae. Recently Rosenberg (115) has segregated from the last a fourth family, the Dasyaceae (*Dasya*, *Dasyopsis*, *Heterosiphonia*), distinguished largely by the sympodial construction of the vegetative system. The astounding diversity in vegetative organisation, despite a re-

<sup>10</sup> The more important Cryptonemiales are: Gloeosiphoniaceae, Callymeniaceae, Grateloupiaceae, Dumontiaceae, Cruoriaceae, Rhizophyllidaceae, Squamariaceae and Corallinaceae; Gigartinales: Nemastomaceae, Furcellariaceae, Solieriaceae, Rhabdoniaceae, Rhodophyllidaceae, Hypneaceae, Plocamiaceae, Sphaerococcaceae, Gracilariaceae, Phyllophoraceae and Gigartinaceae.



markable degree of uniformity in the structure of the reproductive organs and in the post-fertilisation events, suggests that the Ceramiales are a long-established group, the members of which have undergone pronounced evolutionary developments in the vegetative system in comparatively recent times.

#### CLASSIFICATION OF THE MYXOPHYCEAE

##### (Cyanophyceae, Schizophyceae, Phycochromophyceae)

The broad classification of blue-green algae adopted by Kirchner (62) in the first edition of the "Natürliche Pflanzenfamilien" and in part based on that of Thuret (151), was universally accepted during the earlier part of this century (159, 161). Kirchner subdivided the Schizophyceae, as they were called in the "Natürliche Pflanzenfamilien", into Coccogoneae with the families Chroococcaceae and Chamaesiphonaceae, and Hormogoneae (Hormogoneales of later authors) including the more definitely filamentous members of the class. The latter were grouped into Pilonemateae (with Oscillatoriaceae, Nostocaceae, Scytonemataceae and Stigonemataceae) and Trichophoreae (with Rivulariaceae and Campotrichaceae), according as hairs terminating the trichomes were absent or present, but this distinction, which lays stress on a minor character, has rightly met with little favour. Setchell and Gardner (130) subdivided the Hormogoneales into Homocystineae and Heterocystineae, the former including only the Oscillatoriaceae, and this grouping is followed by G. M. Smith (135). It should be noted, however, that by no means all Heterocystineae possess heterocysts.

Increasing knowledge of the genera classed in the Chamaesiphonaceae led to recognition of more fundamental differences from Chroococcaceae than could be adequately expressed by inclusion of these two families in a common group, and so from 1925 (49, 162) we find the three orders Chroococcales, Chamaesiphonales and Hormogoneales figuring in the classification of Myxophyceae (*cf.* also 164).

Geitler's (49) detailed consideration of Myxophyceae, in preparation for his treatment of the class in Rabenhorst's "Kryptogamenflora" (50), clarified the classification within these three orders. As a result of his own contributions, especially those relating to Chamaesiphonales (48), and by bringing to the front a considerable number of tropical Hormogoneales described earlier by Borzi,

Geitler demonstrated an appreciably wider range in morphological construction among blue-green algae than had been recognised in previous taxonomic works. Among Chroococcales he distinguished the largely palmelloid Chroococcaceae (*Chroococcus*, *Gloeocapsa*, *Aphanocapsa*, etc.) from a number of colonial forms showing something of a filamentous tendency, the Entophysalidaceae (49, 235), including amongst others the important marine lithophytes *Entophysalis* and *Platoma*. To Geitler we also owe recognition of several different developmental series among Chamaesiphonales, as exemplified by the distinction, as separate families of the order, of the Dermocarpaceae, Chamaesiphonaceae and Pleurocapsaceae.

The heterogeneity of the group of forms classed in the Chamaesiphonales has led the writer (44, 46) to separate the Pleurocapsaceae and Hyellaceae as Pleurocapsales from the series of essentially unicellular epiphytes included in Dermocarpaceae and Chamaesiphonaceae, for which the old order Chamaesiphonales is retained. The Chamaesiphonales, in this more limited sense, are probably a branch-line from the Chroococcales, since certain species of *Dermocarpa* are closely related to *Chroococcus* and its immediate allies (44, 136); the most important difference lies in the epiphytic habit and consequent polarity. Forms allied to *Dermocarpa* in which retention and uniseriate production of endospores has become the rule, have developed a pseudo-filamentous habit (*Stichosiphon* and ? *Endonema* (101)). On the other hand, there is every reason to believe that the characteristic exospore-formation of *Chamaesiphon* is derived from the process of endospore-formation seen in certain species of *Dermocarpa* (50, 416).

The commoner members of the Pleurocapsaceae (*Radaisia*, *Pleurocapsa*, *Oncobyrsa*) are filamentous forms and, moreover, are typical examples of that variant of the heterotrichous habit that results in the formation of compact crusts. They are in fact a marked vegetative parallel to the Myrionemataceae among Phaeophyceae and to the Cruoriaceae and Squamariaceae *inter alia* among Rhodophyceae. The former inclusion of Pleurocapsaceae among Chamaesiphonales rested essentially on joint possession of endospores. These reproductive bodies, however, occur also in diverse Chroococcales and in *Herpyzonema* among Hormogoneales (158, 36). Their pronounced filamentous character and heterotrichous habit separate the Pleurocapsales sharply from the Chamaesiphonales, and it may

be doubted that there is any close affinity between them. Certain Pleurocapsaceae (*Xenococcus*, *Chroococcopsis*) exhibit a more or less pronounced tendency towards loss of the filamentous habit (*cf.* Chaetosphaeridiaceae among Chaetophorales).

The Hyellaceae (included in Pleurocapsaceae by Geitler, (50)) comprise a series of mainly lime-boring forms, of which *Hyella* has long been known. In recent years the family has been enriched by the description by Ercegović (29, 30), from the coasts of Dalmatia, of a number of other endolithic genera (*Scopulonema*, *Dalmatella*, *etc.*) which appear to be widespread in the Mediterranean area (4, 55; 35). Although their generic status has been disputed (88), they indicate the existence of a considerable diversity in differentiation, especially of the endolithic system. The Hyellaceae are parallel, in both mode of occurrence and vegetative organisation, to the Gomontieae among Chaetophorales, and, like the latter, are characterised by the fact that the penetrating threads arise from the under side of the prostrate system, which inhabits the surface or surface layers of the substratum.

In his preliminary review Geitler (49, 252; *cf.* also 27) distinguished two series of Hormogoneales, the Nostocales and Stigonematales. The former included all the Hormogoneae of Thuret, the latter the forms grouped by Kirchner in Stigonemataceae, now classed in a number of different families and much enriched by adoption of Borzi's genera referred to above. This classification into Nostocales and Stigonematales was not maintained in Geitler's later work (50, 105), although it has been resuscitated by the writer (44, 46), partly on the basis of other considerations.

The Stigonematales are distinguished from other heterocystous Hormogoneae not only by the abundant occurrence of true branching but also by their heterotrichous habit. Moreover, they usually possess definite pit-connections between the cells, and the threads show a considerable tendency towards apical growth. Four or more families are readily distinguished (50, 457; 44, 142). The heterotrichy is clearly differentiated in the Pulvinulariaceae, Capsosiraceae and Stigonemataceae, but is lacking in the specialised family Nostochopsidaceae (*Nostochopsis*, *Mastigocoleus*), distinguished by the frequent position of the heterocysts at the ends of short laterals. The least specialised members are comprised in the Pulvinulariaceae and Capsosiraceae, among which *Pulvinularia* and

*Stauromatonema*, respectively, exemplify a crust-development, analogous to that seen in many Pleurocapsaceae, while *Hyphomorpha* (Pulvinulariaceae) develops a prostrate system only and constitutes a parallel to similar forms in the heterotrichous groups of other classes of algae. A greater specialisation is evident among many of the less advanced Stigonemataceae (*Hapalosiphon*, *Fischerella*, *Westiella*) where the erect threads of the heterotrichous filaments are commonly little branched, usually differ from the prostrate ones in their narrower and longer cells and alone produce hormogonia, whilst the akinetes found in several genera are formed by the cells of the prostrate threads. The multiserial character of the trichomes that characterises most species of *Stigonema* is foreshadowed in *Fischerella*.

Classification of the Nostocales remains much as it was in Kirchner's day. No satisfactory basis has so far been found for a further subdivision of the families Oscillatoriaceae, Nostocaceae, Scytonemataceae and Rivulariaceae, which are on the whole clearly defined and still retain much the same limits as were given them by the older systematists. The Camptotrichaceae of West (163, 268) have, however, been suppressed; the rare non-heterocystous *Hammatoidea*, with trichomes tapering at each end, is now included in Rivulariaceae (49, 269), while *Camptothrix* itself remains a genus *incertae sedis*.

The three genera *Aulosira*, *Microchaete* and *Hormothamnion*, grouped in a subdivision of Nostocaceae by Kirchner (62, 76), have been referred to a separate family (Microchaetaceae) by Geitler (50, 664), although the family appears quite heterogeneous and is of doubtful value. The only feature that *Aulosira* has in common with *Microchaete* is the firm, well defined sheath around the trichomes; in other respects it is much like *Anabaena*. *Microchaete*, in its possession of basal heterocysts, approximates to *Cylindrospermum*, while the marine *Hormothamnion* represents an altogether distinctive type amongst Nostocaceae.

A peculiar line of development among Scytonemataceae is that comprising *Brachytrichia* and a few other little-known genera (*Kyrtuthrix* (29); *Herpyzonema* (158)). With increasing knowledge these may provide the basis for an additional family of Nostocales. The Brachytrichieae are essentially characterised by a modification of that mode of origin of geminate false branches involving



a process of loop-formation which has been observed in certain kinds of *Scytonemas*. In the former, however, the loops usually remain intact (28; 49, 217) and there is a tendency for one arm of the loop to continue growth so that it later appears at the apex of the V-shaped lower portion. A similar method of branching is sometimes found in the hot-spring alga *Mastigocladus*, and, for this reason, Geitler (49, 263; 50, 553) established a family Mastigocladaceae to include this genus, as well as the Brachytrichieae. *Mastigocladus*, however, has very little in common in other respects with the Brachytrichieae and in certain stages shows true branching and a marked resemblance in habit to *Hapalosiphon* (34, 456; 36, 179). For the present it is best referred to Stigonemataceae.

#### CLASSIFICATION OF DIATOMS

##### (Bacillariales, Bacillariophyceae)

The present-day classification of this highly specialised group still follows essentially that of Schütt (127) in the first edition of the "Natürliche Pflanzenfamilien". He distinguished the two main subdivisions, Centricae and Pennatae, on the basis of the general symmetry relations of the cells, and these have since been recognised as independent orders (57; Centrales and Pennales of Karsten (60)). The Centrales are classed in four families, according as the cells are shortly cylindrical or discoid (Discaceae, e.g., *Cyclotella*, *Melosira*), elongate-cylindrical with numerous intercalary bands (Soleniaceae, e.g., *Corethron*, *Rhizosolenia*), box-shaped with valves having two or more poles (Biddulphiaceae, e.g., *Chaetoceras*, *Isthmia*, *Triceratium*), or naviculoid but with radially arranged markings (Rutilariaceae with *Rutilaria*).

Schütt recognised four series of pennate diatoms (Fragilarioideae, Achnanthoideae, Naviculoideae, Surirelloideae). Karsten's (60) and Hustedt's (57) more recent schemes introduce a greater degree of subdivision which, like that of Schütt, is based essentially on the presence or absence of a raphe in the valves, and its mode of differentiation. They distinguish four main groups of Pennales, the Araphideae (*Fragilaria*, *Synedra*, etc.) in which the valves possess only a pseudoraphe, the Raphidioideae (*Eunotia*, *Peronia*) with a raphe limited to a short extension from the polar nodules, the Monoraphideae (*Achnanthes*, *Cocconeis*, *Rhoicosphenia*) with a fully developed raphe on one valve only, and the Biraphideae with

a raphe on both valves. The Araphideae (Schütt's Fragilarioideae) are probably an artificial group, in some members of which the absence of the raphe may be primitive, whilst in others (*e.g.*, *Synedra*) it has possibly been secondarily lost, perhaps in adaptation to a planktonic existence. The status of the Raphidioideae is uncertain, but it is perhaps more probable that they are Monoraphideae (*Peronia*) and Biraphideae (*Eunotia*) in which the raphe is in course of reduction.

The Biraphideae include a large diversity of genera which are grouped as Naviculoideae, Epithemioideae, Nitzschioideae and Surirelloideae. The Naviculoideae (*Navicula*, *Pinnularia*, *Gomphonema*, *etc.*) are distinguished from the Epithemioideae (*Denticula*, *Epithemia*, *etc.*) by the position and nature of the raphe. In the former it occupies the apical (sagittal) axis and consists in each valve of two longitudinal clefts which are linked in the region of the central nodule. In the Epithemioideae, on the other hand, the raphe lies outside the apical axis, sometimes on an eccentric keel, and takes the form of a canal running longitudinally through the membrane of the valve. A similar canal-raphe is met with in the Nitzschioideae (*Nitzschia*, *Hantzschia*, *etc.*), but here it is always situated in a keel which is often eccentric; the raphe is here provided with the characteristic carinal dots, representing apertures on the inner surface of the raphe or the strips of membrane intervening between these apertures. In the Surirelloideae (*Surirella*, *Cymatopleura*, *etc.*), lastly, the canal-raphe occupies two lateral wings on the valves and is connected by obvious canals with the protoplast.

The relation of the two main orders of diatoms to one another remains as obscure as ever, although the suggestion of a possible distinct origin (92, 194; 108) does not at present find much favour. As our knowledge of Centrales and Pennales increases, the contrasts between the two series become more marked. Karsten (60, 182) was of the opinion that production of auxospores by sexual fusion in the majority of the Pennales resulted from the acquisition of motility by the latter, since the scanty data relating to Araphideae (*cf.* 41, 620) suggest that auxospore formation may here take place in a manner similar to that observed in certain Centrales. Karsten believed that the Tabellariaceae were allied to some of the Centrales by way of such forms as *Terpsinoë* which possess naviculoid valves

provided with numerous transverse septa. Geitler's (51) recent demonstration that in *Synedra ulna* auxospores are formed by conjugation of gametes from distinct individuals, not only necessitates reexamination of other Araphideae by modern methods, but suggests that some of them at least are closely related to Pennales provided with a raphe. There is in fact no adequate evidence to warrant the belief that the Araphideae are primitive among Pennales; some, and perhaps all of them, may equally well be reduced forms.

It may be doubted that, with the data at present available, it is justifiable to regard Centrales and Pennales as anything more than possible divergent lines of development from some common remote ancestry. That they are derived from a flagellate source, as many believe, because of the occurrence of swarmers in Centrales and the occasional observation of contractile vacuoles in Pennales (51, 555; 106), remains to be more clearly established. Until more is known of the methods of reproduction of Centrales and of the Araphideae it is not profitable to discuss the matter further.

#### INTERRELATIONSHIPS OF THE VARIOUS ALGAL CLASSES

Pascher (95, 104) classes the algae as a whole as follows:—

- I. Chrysophyta.
  - A. Chrysophyceae.
  - B. Diatomeae (Bacillariales of other authors).
  - C. Heterokontae (Xanthophyceae of this article).
- II. Phaeophyta (Phaeophyceae).
- III. Pyrrophyta.
  - A. Cryptophyceae.
  - B. Desmokontae.
  - C. Dinophyceae.
- IV. Euglenophyta (Euglenineae).
- V. Chlorophyta.
  - A. Chlorophyceae.
  - B. Conjugatae.
- VI. Charophyta (Characeae).
- VII. Rhodophyta (Bangineae and Floridineae).
- VIII. Cyanophyta (Myxophyceae).

Each of these main groups is regarded as having the same status as Bryophyta and other so-called "higher" groups, a point of view

which it is not the province of this article to discuss. Smith (136) follows this grouping of Pascher.

The combination of Chrysophyceae, Xanthophyceae and diatoms in a common group, Chrysophyta, was suggested by Pascher in 1914 (95) and more fully substantiated in 1921 (97). He bases his view of the affinity between the three classes on the possession of a number of common characteristics; (*a*) preponderance of yellow or brown carotenoid pigments in the chromatophores, (*b*) absence of starch and occurrence of oil as a frequent photosynthetic product, (*c*) presence of leucosin, characteristic of Chrysophyceae, in certain diatoms (68) and Xanthophyceae (102), (*d*) frequent deposition of silica in the cell membranes (mainly in the cysts of Xanthophyceae and Chrysophyceae), (*e*) bipartite nature of the cell wall seen in the diatom frustule, in the vegetative cells and resting spores of diverse Xanthophyceae, and in the cysts of Chrysophyceae, (*f*) presence of envelopes composed of numerous pieces in Xanthophyceae (*Tribonema*, *Ophiocytium*), Chrysophyceae (*Dinobryon*) and diatoms (intercalary bands), (*g*) similarity between the cysts of Chrysophyceae and the endogenous cysts of the diatom *Chaetoceras*, (*h*) occurrence of endogenous cysts also in certain Xanthophyceae (*Chloromeson* (102, 405)), and (*i*) presumed flagellate ancestry of diatoms. There appears to be substantial evidence in favour of close affinity between the flagellate members of Xanthophyceae (*Chloromeson*, *etc.*) and Chrysophyceae (especially the Ochromonadeae).

Diatoms are assumed to have the same status among Chrysophyta as the Conjugales have among Chlorophyta, but it must be emphasised that they stand far more isolated than do the Conjugales among Chlorophyta. The Pennales at least are diploid forms, with a highly derived sexual process, whereas the very scanty data we have in relation to sexuality in Xanthophyceae and Chrysophyceae point to their being haploid forms. Despite obvious similarities between the three classes in respect of membrane-structure, which may be homoplastic, there is nothing even approaching the astounding complexity of the wall attained in both groups of diatoms. The wide gap between the latter and the members of the other two classes renders their classification in one common group very problematic.

In the Pyrrophyta, Pascher (99, 51) regards the Desmomonada-ceae as comprising the most primitive forms, and he suggests a deri-



vation of the Cryptomonadales from them by development of a dorsoventral organisation and of the longitudinal furrows which are so evident in the cells of *Cryptomonas*, for instance. In *Pleromonas* and *Haplodinium* the cells exhibit an apical incision which is regarded as the precursor of the furrows typical of Cryptomonadales, but the significance of these furrows is unknown and it may be that too much stress is being placed on this character. The Desmomonadaceae, however, show appreciable resemblances to Cryptomonadales in general organisation, in the presence of two dissimilar band-shaped flagella, in pigmentation, and in the possession of solid photosynthetic products.

A relationship between Dinoflagellata and Cryptomonadales was accepted by Klebs (64) and is also supported by Lindemann (85). In particular the Nephroselmidae (*Protochrysis*, *Nephroselmis*) among the latter, where the flagella are attached laterally and the furrows run more or less transversely, invite comparison with such a genus as *Hemidinium* among Dinoflagellata. The Nephroselmidae demonstrate that in the evolution of the Cryptophyceae there has been a shifting of flagella and furrow to the ventral surface, and such transposition probably also occurred in the evolution of the Dinoflagellata. The varied position of the flagellar apertures and of the furrow system on the ventral surface among Gymnodinioideae at least shows that shifting must often have occurred during evolution within the order Dinoflagellata itself. The exact origin of the type of cellular organisation typical of the latter is not clear, however, and there is no satisfactory basis for a direct connection with forms like the Desmomonadaceae. The undoubted resemblances between Cryptomonadales, Desmomonadales and Dinoflagellata are not, in the present state of our knowledge, of such a nature as to render homoplasy out of the question, and their classification in a common group is probably premature. On the other hand, the Dinophysiales among Desmokontae show an appreciable degree of approximation to some of the armoured Dinoflagellata, and an origin of Desmokontae and Dinokontae from a common stock appears highly probable.

Several authorities have hesitated to abandon altogether the former classification of the members of Xanthophyceae among the Chlorophyceae. Thus, West (161, 153) included the Heterokontae as a division of Chlorophyceae and Printz (113) does the same.

All evidence, however, indicates that Xanthophyceae and Chlorophyceae are perfectly distinct evolutionary series. Steinecke's (138) interpretation of the former as a reduction-series, commencing with the filamentous forms which are supposed to be derived from *Microspora*, has no real basis in fact. Chodat's (21) inclusion of Heterokontae, Peridinieae, Bacillariales and Euglenineae among Phaeophyceae ignored many securely established facts and requires no serious consideration. No justification can be found for the reference of Peridinieae, Bacillariae and Conjugatae to a common group Zygomphyta by Wettstein (164), since these three series have no features in common with one another.

It may be doubted that any real progress is achieved by endeavouring to bring together any of the eleven classes distinguished by the author (41). The time is certainly not yet ripe for phylogenetic speculations like those of Steinecke (137) and Zimmermann (168), and, unless the fossil record furnishes data of a kind different from those it at present provides, it may be questioned whether such speculations will ever fulfill a useful purpose.

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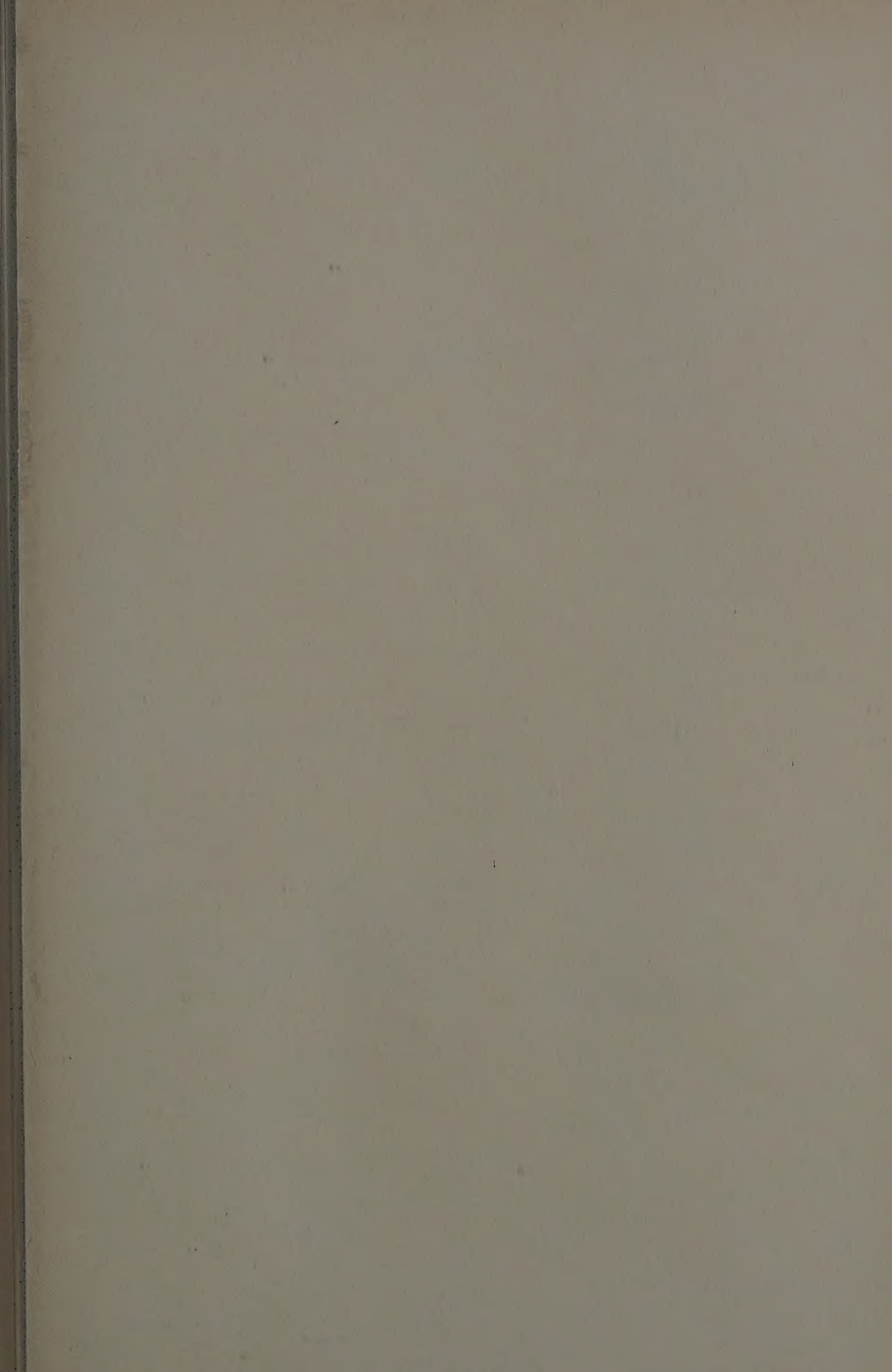


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Plant Disease Introduction .....	W. A. McCUBBIN <i>Bureau of Entomology and Plant Quarantine</i>
Plant Oils .....	J. B. McNAIR <i>Field Museum, Chicago</i>
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# Proposed Future Contents of THE BOTANICAL REVIEW

## *Articles received and awaiting publication*

Control of Noxious Plants .....	H. K. WILSON University of Minnesota
Recent Studies on the Inheritance of Size and Shape in Plants .....	H. H. SMITH Bureau of Plant Industry
Radiation and Plant Respiration .....	R. L. WEINTRAUB Smithsonian Institution
Plant Microfossils .....	L. R. WILSON Coe College
Fungus and Bacterial Diseases of Insects as Factors in Biological Control .....	H. S. FAWCETT University of California Citrus Experiment Station
Heterosis .....	W. G. WHALEY Barnard College

## *Articles arranged for most recently*

Taxonomy of North American Fresh-Water Algae	L. H. TIFFANY Northwestern University
Laboratory Testing of Spraying and Dusting Fungicides .....	J. G. HORSFALL Connecticut Agriculture Experiment Station
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## *Articles in course of preparation*

Endomitosis .....	A. LORZ Seton Hall College
The Male Gametophyte of Angiosperms .....	A. GERSHOY University of Vermont
Techniques for Aseptic Growth of Plants .....	L. C. KNORE Cornell University
The Cytology of Fertilization in Angiosperms ....	L. E. ANDERSON Duke University
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Anthocyanin Pigments .....	F. BLANK Switzerland
The Genetics of Pollen Tube Growth .....	J. T. BUCHHOLZ University of Illinois
Sexuality and Genetics of Algae.....	H. BOLD and W. G. WHALEY Columbia University
The Angiosperm Embryo Sac .....	EMMA L. FISK University of Wisconsin
Cytogenetics of Nicotiana .....	T. H. GOODSPEED University of California
Tundra Vegetation .....	R. F. GRIGGS
Cytology and Genetics in Relation to Taxonomy ..	C. L. HUSKINS McGill University
A Critical Survey of the Present Status of Plant Embryology .....	D. A. JOHANSEN Stanford University, Cal.
Genetics of Neurospora .....	C. L. LINDEGREN Washington University

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